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Statistical Analysis of the Spatial and Temporal Variability of the Ratio Chlorophyll A to Phytoplankton Cell Volume in Saginaw Bay, Lake Huron

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16. ABSTRACT

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The procedures employed included t-tests, analysis of variance and polynomial regression. The hypothesis that the natural log of the ratio of chlorophyll a to cell volume was constant in time was tested on six different sampling station groupings representing various spatial divisions of Saginaw Bay. In all cases, this ratio was found to vary significantly at the 95% confidence level. The variability of the ratio decreased when only data from the outer portion of Saginaw Bay were used. Greater than 60% of the variability of the ratio can be removed by using a linear correlation of the natural log chlorophyll a cell volume ratio with the fraction of diatom cell volume.

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STATISTICAL ANALYSIS OF THE SPATIAL AND TEMPORAL VARIABILITY OF THE RATIO CHLOROPHYLL *A* TO PHYTOPLANKTON CELL VOLUME IN SAGINAW BAY, LAKE HURON

David M. Dolan[1], Victor J. Bierman, Jr., Merlin H. Dipert[2] and Raymond D. Geist
U.S. EPA
Large Lakes Research Station
Grosse Ile, Michigan 48138

ABSTRACT. *Chlorophyll a has traditionally been used as an indicator of phytoplankton concentration in natural waters. This parameter has also been widely used by phytoplankton modelers for the purpose of comparing model output with field data. Examination of 1974 field data from Saginaw Bay indicated that chlorophyll a concentrations were inconsistent with phytoplankton cell volume concentrations. Statistical procedures were employed to determine the significance and source of the observed variability in the ratio of chlorophyll a to cell volume concentrations.*

The procedures employed included t-tests, analysis of variance and polynomial regression. The hypothesis that the natural log of the ratio of chlorophyll a to cell volume was constant in time was tested on six different sampling station groupings representing various spatial divisions of Saginaw Bay. In all cases, this ratio was found to vary significantly at the 95% confidence level. The variability of the ratio decreased when only data from the outer portion of Saginaw Bay were used. Greater than 60% of the variability of the ratio can be removed by using a linear correlation of the natural log chlorophyll a to cell volume ratio with the fraction of diatom cell volume.

INTRODUCTION

Three frequently used indicators of algal abundance are 1) chlorophyll *a* concentrations, 2) cell counts and, 3) cell volumes. Each indicator has its advantages and disadvantages, but, ideally, each is a measure of the same quantity: the amount of phytoplankton biomass present in a sample.

Chlorophyll *a* concentrations provide quantitative information about the gross amount of phytoplankton present in a sample. Chlorophyll *a* is widely used because of the relative ease with which samples can be obtained and analyzed. A major drawback to this measure of algal biomass is that it does not give information on species or class composition.

Cell counts can be used to study species composition and diversity. Cell count data can be used to detect trends and species shifts. The disadvantages of this indicator include the greatly increased analytical effort required, as compared to chlorophyll *a*, and the difficulty of converting the count data to dry weight or cell carbon as a result of species variations in cell sizes over 3-4 orders of magnitude.

Cell volume data provides all of the information that cell counts do. In addition, reasonable cell carbon and dry weight estimates can be made at the species or functional groups level. However, cell volume information is more difficult to obtain than either of the other indicators. An enormous data reduction effort is necessary, causing a substantial increase in the amount of time before data are available for analysis.

Most limnological studies use one or more of the above indicators to estimate the dry weight of phytoplankton and/or the cell carbon present (Vollenweider, Munawar and Stadelmann 1974, Mullin, Sloan and Eppley 1966). Algal biomass in dry weight per liter can be estimated from chlorophyll *a* concentration by application of a chlorophyll *a* to biomass ratio. Biomass from cell counts can be obtained using a dry weight biomass per cell ratio. Cell volume can be used with an assumed density and a dry weight to wet weight ratio to obtain biomass.

If these algal biomass estimators are equally valid, then the relationship among them should

[1]To whom correspondence should be addressed.
[2]U.S. EPA, Data Processing Branch, Region V, Chicago, Illinois 60604.

remain constant in time. A large body of experimental evidence suggests that this is not the case. Healey (1975) presented data on the chlorophyll content of cultured algae. Chlorophyll was shown to vary from 0.1 to 3.5 percent of algal dry weight depending on nutrient concentrations, light and temperature. Nicholls and Dillon (in press) reviewed the literature and found a range of chlorophyll content of 0.1 to 9.7 percent of fresh weight for natural assemblages. Bogorad (1962) reviewed additional factors that affect cell chlorophyll content such as cell age, sulfur and trace metals. Myers (1946) observed that while cell volume concentrations remain constant with increasing light intensity, chlorophyll and cell number concentrations decrease. Fogg (1975) noted that if individual species in pure culture are being studied then most biomass estimators give useful pictures of abundance. However, when natural populations are encountered the choice of estimator may influence conclusions about the relative importance of different species.

The present study was motivated by the application of a multi-class phytoplankton model to Saginaw Bay (Bierman and Dolan 1976, Bierman *et al.* in preparation). Models based on chlorophyll *a* require only data on that parameter for verification of the calculated phytoplankton standing crops. When multi-class phytoplankton models are used in lake simulations, species specific biomass information is needed for verification. Cell volume measurements are useful for this purpose. The determinations can be made at the species level and then integrated into groups, e.g., diatoms and non-diatoms or diatoms, greens and blue-greens, that correspond to model output.

The variability in estimates of algal biomass can have important implications for mathematical models of phytoplankton growth. The purpose of this paper is to compare chlorophyll *a* and cell volume as estimators of phytoplankton biomass. This is done using a number of statistical tests on an extensive chlorophyll *a* and cell volume data set from Saginaw Bay in 1974. These tests can be used to demonstrate the statistical significance of the variability of chlorophyll *a* to biomass ratios calculated from this data set as well as explain a major part of this variability.

BACKGROUND

Saginaw Bay is a shallow extension of Lake Huron (Figure 1). Excessive chlorophyll concentrations (up to 70 μg/L) are an indication of the eutrophic character of the bay, especially the inner portion.

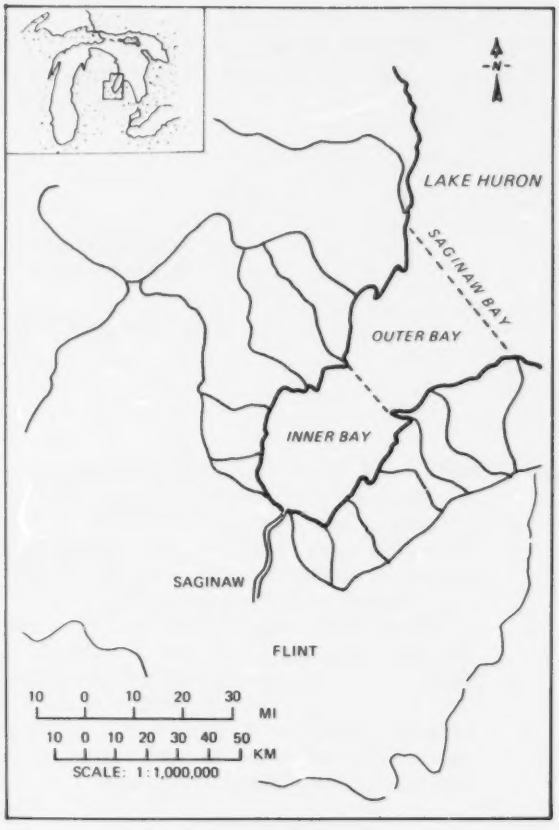

FIG. 1. Saginaw Bay watershed indicating divisions between inner and outer portions of the bay.

However, due to the shallow nature of the bay and rapid flushing from Lake Huron, there is no significant oxygen depletion. The direction of water movement in the bay is generally counterclockwise. Lake Huron water moves in along the north shore of the bay and a mixture of Saginaw River and Lake Huron water moves out along the south shore. The Saginaw River is the primary source of nutrient loading to the bay.

Previous limnological studies on Saginaw Bay have been reviewed by Freedman (1974). Since 1973, the Cranbrook Institute of Science has been conducting extensive water quality surveys on the bay (Smith *et al.* in preparation). These surveys have provided comprehensive water chemistry data that allow the definition of spatial gradients within the bay. In 1974, this survey included 59 sampling stations (Figure 2). This resulted in 111 station-depth combinations for each of 13 cruises. In addition, samples for phytoplankton and zooplankton were taken at each of these stations by the University of Michigan, Great Lakes Research Division.

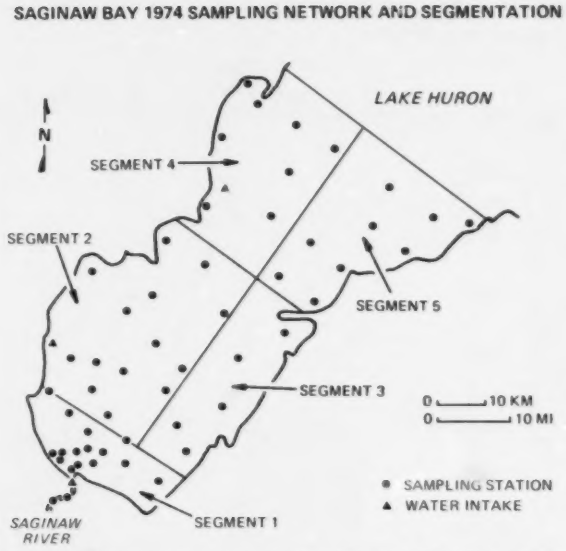

FIG. 2. Segmentation scheme for Saginaw Bay and station locations.

A segmentation scheme, based on observed water movements and gradients of conservative substances, was developed for the purpose of aggregating the Cranbrook stations into groups of similar water quality. Segments 1 through 5 (Figure 2) represent the resulting spatial divisions. Due to the influence of the Saginaw River and the circulation in the bay, Segments 1 and 3 are the most nutrient enriched (Table 1). Segment 4 is most representative of Lake Huron water. A sixth station grouping, the Inner Bay, is a combination of Segments 1 through 3 and is the area to which a multi-class phytoplankton model has been applied (Bierman and Dolan 1976).

As part of the mathematical modeling effort on Saginaw Bay, average chlorophyll *a* and average biomass (from cell volumes) concentrations for inner Saginaw Bay were compared and it was observed that these indicators did not give the same picture of phytoplankton abundance throughout the year (Figure 3). Furthermore, when the ratio of average chlorophyll *a* to average biomass was plotted vs. time (Figure 4a) and compared to a plot of percent composition of phytoplankton crop by cell volume vs. time (Figure 4b), a correlation of the ratio with percent composition was suggested. Given these initial observations, a decision was made to conduct a comprehensive statistical analysis of the spatial and temporal variability of the phytoplankton data in Saginaw Bay.

APPROACH

The statistical tests that were performed included the t-test, the one-way analysis of variance, and three *a posteriori* contrasts. The following is an outline of the test procedure.

1. A transformation of the chlorophyll *a* to cell volume ratio was sought that would be normally distributed.
2. Six different spatial divisions or station groupings of the bay were defined.

TABLE 1. Water quality characteristics of Saginaw Bay - 1974 (Smith et al. *in preparation).*

		Segment 1	Segment 2	Segment 3	Segment 4	Segment 5	Inner Bay*
D.O. mg/ℓ	Mean ± s.d.	10.1 ± 1.6	10.1 ± 2.0	10.1 ± 1.7	11.6 ± 1.8	11.0 ± 1.6	10.1 ± 1.8
	Range	4.7 - 16.0	2.7 - 14.0	7.6 - 14.8	8.8 - 15.5	8.3 - 15.5	2.7 - 16.0
	# of Samples	156	205	50	175	119	411
Chloride mg/ℓ	Mean ± s.d.	22.9 ± 12.9	13.4 ± 5.6	20.0 ± 7.7	7.0 ± 4.0	9.0 ± 4.4	17.9 ± 10.4
	Range	5.4 - 85.4	2.7 - 67.0	6.1 - 40.3	2.9 - 40.0	3.3 - 26.2	2.7 - 85.4
	# of Samples	201	260	68	254	208	529
Chlorophyll *a* (corrected) µg/ℓ	Mean ± s.d.	29.0 ± 14.9	16.3 ± 10.4	24.9 ± 13.4	3.5 ± 2.3	7.7 ± 8.8	22.5 ± 14.1
	Range	1.1 - 74.4	2.3 - 45.7	4.4 - 58.5	.4 - 11.5	.3 - 57.4	1.1 - 74.4
	# of Samples	152	178	54	138	128	384
Total Phosphorus mg/ℓ	Mean ± s.d.	.058 ± .039	.026 ± .013	.037 ± .015	.009 ± .010	.013 ± .016	.038 ± .029
	Range	.002 - .290	.003 - .069	.011 - .081	.002 - .089	.002 - .048	.002 - .290
	# of Samples	109	180	47	157	142	336
Dissolved Silica mg/SiO_2/ℓ	Mean ± s.d.	.88 ± .70	1.05 ± .65	.72 ± .39	1.08 ± .33	.98 ± .42	.95 ± .65
	Range	.07 - 3.94	.05 - 3.69	.05 - 1.87	.07 - 2.03	.04 - 3.17	.05 - 3.94
	# of Samples	200	275	68	256	209	543

*Segments 1, 2 and 3

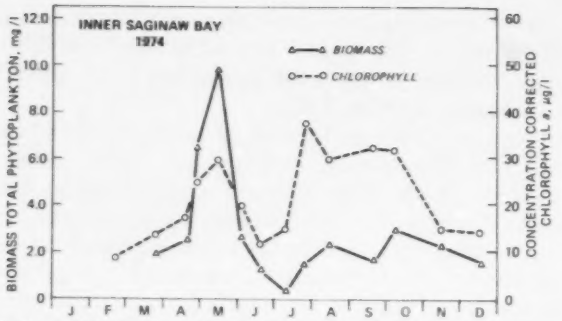

FIG. 3. Phytoplankton abundance in inner Saginaw Bay, 1974 as indicated by chlorophyll a *and biomass.*

3. The t-test was performed on every cruise-pair combination in each of the six different station groupings and the results tabulated.
4. The analysis of variance and contrasts were performed on all the cruises combined and the results tabulated.

Another statistically valid method of demonstrating the variable nature of the chlorophyll *a* to cell volume ratio was to establish a significant functional dependence of the ratio on an independent variable. This method has the added advantage of providing estimates of the reduction in variance of the data when the ratio is correlated with an independent variable. A linear regression was performed with the ratio as the dependent variable and the fraction diatoms by cell volume as the independent variable.

DATA BASE

The chlorophyll *a* and cell volume values used in the calculation of the ratio were obtained from twelve sampling cruises in 1974. Each chlorophyll *a*-cell volume pair was determined from the same sample at a depth of one meter. The sampling and analysis for chlorophyll *a* was performed by the Cranbrook Institute of Science (Smith *et al.* in preparation). The cell count and volume data used to calculate the ratio and the fraction diatoms was produced by University of Michigan, Great Lakes Research Division (Stoermer *et al.* in preparation).

The chlorophyll *a* to cell volume ratio was formed for each station grouping by calculating the ratio for individual stations and then calculating an average for the station grouping for each cruise. Analysis of the data has indicated that although field data for chlorophyll *a* from the same station grouping are normally distributed, cell volume data are not. Instead, these data appear to

FIG. 4a. Chlorophyll a *to biomass ratio vs. time for inner Saginaw Bay, 1974.*

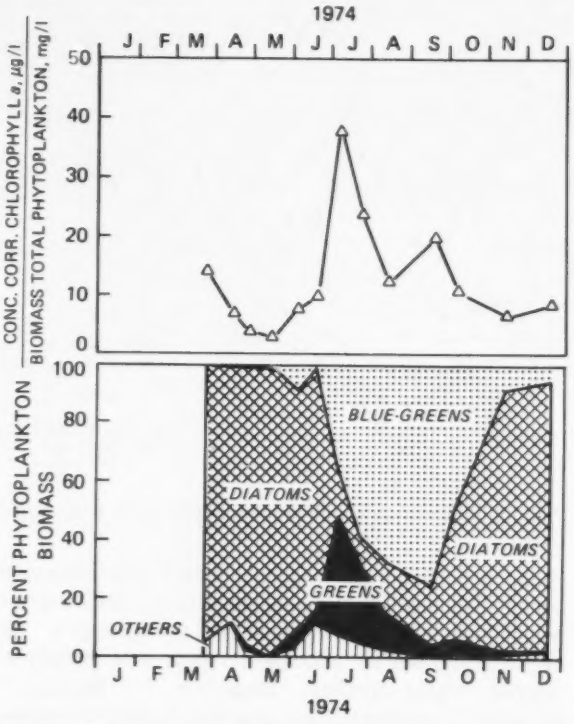

FIG. 4b. Composition of phytoplankton crop vs. time for inner Saginaw Bay, 1974.

have a skewed distribution. The resulting chlorophyll *a* to cell volume ratio would, therefore, not be normally distributed and some transformation of this ratio would be necessary in order to apply the usual statistical tests. The quantity natural logarithm of the chlorophyll *a* to cell volume ratio (ln[chl *a*/cell volume]) was found to best approximate normal behavior. The cell volumes have been converted to dry weights by the application of a constant conversion factor. This does not affect the results. The quantity referred to as the ratio in the rest of this paper is the natural logarithm of the chlorophyll *a* to biomass ratio.

STATISTICAL METHODOLOGY

Much of the statistical analysis was performed using SPSS (Statistical Package for the Social Sciences), (Nie *et al.* 1975). A pairwise t-test was conducted using the ratio defined above for different cruise pairs. The "student's" t and probability levels were computed in order to test whether or not the difference between ratios for two different cruises was significant.

A one-way analysis of variance was performed using the ratios for all cruises. The hypothesis that the means for all the cruises for a given station grouping were not significantly different from one another was tested. In addition, three *a posteriori* contrasts were performed on the data which divided the cruises into homogeneous subsets. The difference in the means of any two cruises in a subset was not significant at the 95% confidence level. The three contrasts used were:

1. Least Significant Difference Test
2. Duncan's Multiple Range Test
3. Student-Newman-Keuls Procedure

TABLE 2. T-tests results for the natural logarithm of the ratio of chlorophyll a to biomass at the 95% confidence level.

Grouping	Maximum Sample Size	Percent of Cruise Pairs That Were Significantly Different
Inner Bay	35	75.8
Segment 1	14	74.2
Segment 2	16	71.2
Segment 3	5	31.8
Segment 4	10	29.1
Segment 5	9	32.7

TABLE 3. Results of analysis of variance for natural logarithm of the ratio of chlorophyll a to biomass.

Station Grouping	F-Value	# of Homogeneous Subsets From Contrast		
		Duncan's	Student-Newman-Keuls	Least Significant Difference
Inner	42.8	8	7	8
Segment 1	26.2	5	4	7
Segment 2	17.0	5	6	7
Segment 3	5.6	4	2	4
Segment 4	4.1	3	2	3
Segment 5	3.7	4	3	3

Finally, stepwise polynomial regressions were performed on the ratio to correlate this variable with the fraction of diatoms present on a cell volume basis. A significant correlation was taken to be evidence that the ratio was not constant.

RESULTS

The results of the t-tests between cruise pairs indicated considerable differences in the ratio in the Inner Bay and in Segments 1 and 2 (Table 2). The analysis of variance indicated that the ratio was not constant with 95% confidence for all station groupings (Table 3). The three *a posteriori* contrasts divided all the cruises into at least 2 homogeneous subsets for each station grouping.

The results of the polynomial regressions are summarized in Table 4. The ratio was found to be highly correlated with fraction diatoms by cell volume. The coefficients of the polynomial for the ratio vs. fraction diatoms by cell volume correlation as well as the standard error of these coefficients and the F ratio for each station grouping are given in Table 5.

TABLE 4. Summary of r values from polynomial regression of natural logarithm of the ratio of chlorophyll a to biomass vs. fraction diatoms for Saginaw Bay, 1974.

Station Grouping	r Values for Linear Regression (Dependent Variable) and the Fraction Diatoms	
	(By Volume)	(By Count)
Inner Bay	.892	.808
Segment 1	.840	.690
Segment 2	.879	.809
Segment 3	.908	.788
Segment 4	.474*	.386*
Segment 5	.808	.704

*Not significant at the 95% confidence level.

DISCUSSION

The results of the pairwise t-tests cannot be taken as rigorous proof that the ratio is not constant. These tests were included mainly for the qualitative information that they provide. However, the question of spatial variability can be addressed to a certain degree with these results. The ratio is more

TABLE 5. Linear correlation of natural logarithm of the ratio of chlorophyll a to biomass vs. fraction diatoms by cell volume.

Segment	Intercept	Standard Error of Intercept	Slope	Standard Error of Slope	Correlation Coefficient	F Ratio For Reduction in Variance
Inner	3.35	.213	-1.96	.315	.892	38.8
1	3.31	.288	-2.04	.417	.840	23.9
2	3.37	.208	-1.96	.337	.879	33.9
3	3.49	.228	-2.28	.334	.908	46.8
4	2.74	.542	-1.19	.738	.474	2.60*
5	2.83	.244	-1.79	.435	.808	16.9

*Not significant at the 95% confidence level.

constant throughout the year for Segments 3-5 than the other station groupings (Table 2). This result would have more meaning if it were not for the fact that the maximum sample size for each cruise is considerably less for these segments. At any rate, there does seem to be spatial variability and this can be investigated further with more rigorous tests.

The greater the F value in Table 3, the greater the confidence that the ratio is not constant. Segments 3, 4 and 5 have the lower F values, with Segment 3 having the highest of the group, despite the low sample size for this segment. Segments 4 and 5 represent outer Saginaw Bay and are considerably less enriched than the Inner Bay. As a consequence, the chlorophyll *a* and the biomass present in a sample will be less than in the Inner Bay, and differences between the two measures will be less significant, especially in an analysis of variance test.

Examination of the values of the ratio for all cruises for the Inner Bay and of the results of the Duncan's multiple range contrast for these data suggests a quadratic relationship with time (Table 6). As the year progresses, the ratio first increases, then decreases with the maximum value occurring in the middle of the year, at Cruise 10. The cruise subsets also are often composed of very early or very late cruises (i.e., subset 3).

The quadratic behavior of the ratio with time is analogous to the species succession in many eutrophic water bodies. First diatoms dominate, then blue-greens are predominant, and finally diatoms return. This similarity suggests a direct linear relationship of the ratio with fraction diatoms (Table 4).

For each station grouping, the ratio was better correlated with fraction of diatoms by cell volume than by cell count. This result is not unreasonable, since cell count information does not address size differences among species which would affect chlorophyll *a* content.

The ratio in Segment 4 could not be correlated with fraction diatoms (Table 4). This result is in agreement with the pairwise t-test and the analysis of variance results. The problem can be examined further by a comparison of the range of fraction of diatoms for Segment 4 with the range for the Inner Bay (Table 7). A considerably greater fraction of diatoms was found in Segment 4 for most cruises than in the Inner Bay. If the square of the correlation coefficient (reduction in variance) is considered to be an indication of the percent of variation that is reduced by going from a mean of all cruises to a linear correlation with fraction of diatoms, then a significantly lower reduction in variance would be expected in Segment 4 than in the Inner Bay where fraction of diatoms has much greater variation. In fact, the reduction in variance for the linear regression of the ratio with fraction of diatoms by cell volume in Segment 4 is 22.4% as compared with the Inner Bay which is 79.5%.

This last result can be compared with that obtained for Loch Creran in Scotland by Tett *et al.* (1975). Spring chlorophyll, cell carbon and nutrient concentrations were measured 19 times between February and April 1973. The cell chlorophyll content was observed to depend on cell nutrient content. During the observation period, diatoms were the dominant algal group. Therefore, variation due to changing diatom percentages was not a factor in this experiment. This suggests that the variability of the ratio in Segment 4 could possibly also be explained by nutrient availability or some combination of fraction of diatoms and nutrient concentration. Hecky (1975) found substantially lower chlorophyll to biomass ratios in certain regions of Southern Indian Lake in Manitoba. Since the entire lake had a similar algal composition and was dominated by the diatom *Melosira*, the lower

TABLE 6. Values of natural logarithm of the ratio of chlorophyll a to biomass and results of Duncan's multiple range contrast for Inner Bay.

Cruise	Date	Sample Size	Mean	Standard Error of Mean
5	4/17/74	23	1.86	0.13
6	4/28/74	35	1.19	0.11
7	5/13/74	32	1.01	0.11
8	6/3/74	34	1.72	0.12
9	6/18/74	35	2.21	0.13
10	7/8/74	30	3.47	0.17
11	7/25/74	31	2.74	0.08
12	8/13/74	32	2.48	0.06
13	9/18/74	34	2.94	0.08
14	10/6/74	34	2.37	0.06
15	11/11/74	20	1.95	0.09
16	12/17/74	10	2.20	0.19

Subset 1	Cruise #	7		6	
	Mean	1.01		1.19	
Subset 2	Cruise #	8	5	15	
	Mean	1.72	1.86	1.95	
Subset 3	Cruise #	5	15	16	
	Mean	1.86	1.95	2.20	
Subset 4	Cruise #	15	16	9	
	Mean	1.95	2.20	2.21	
Subset 5	Cruise #	16	9	14	12
	Mean	2.20	2.21	2.37	2.48
Subset 6	Cruise #	12	11		
	Mean	2.48	2.74		
Subset 7	Cruise #	11	13		
	Mean	2.74	2.94		
Subset 8	Cruise #	10			
	Mean	3.47			

chlorophyll to biomass ratios were attributed to nutrient poor conditions.

CONCLUSIONS

As the results of the analysis of variance indicate, the chlorophyll *a* to biomass ratio cannot be taken to be constant throughout the year in Saginaw Bay. Therefore, these quantities cannot be considered to be equivalent estimators of phytoplankton abundance. A large part of the variation in the ratio can be explained by a linear correlation of the logarithm of this ratio with the fraction of diatoms present.

For all station groupings, using the fraction of diatoms by cell volume resulted in a better correlation than using the fraction of diatoms by cell count. The procedures used in this study were repeated on the chlorophyll *a* to cell count ratio. While significant differences were seen in the ratios

TABLE 7. Fraction diatoms by cell volume for segment 4 and the Inner Bay.

Cruise #	Segment 4	Inner Bay
5	.875	.881
6	.910	.951
7	.985	.959
8	.673	.897
9	.918	.687
10	.632	.170
11	.292	.196
12	.415	.204
13	.620	.286
14	.747	.477
15	.863	.878
16	No Data	.920

from cruise to cruise, no correlation with fraction of diatoms present could be obtained.

The assumption of a constant ratio becomes more valid if only data for the less enriched outer Saginaw Bay are considered. This suggests that the types of phytoplankton in the water body and its state of enrichment are the important factors in determining whether the constant ratio assumption is valid. In enriched waters, the differences between algal biomass estimators are magnified by the large standing crops. In cleaner waters, these differences are less significant. The fact that the ratio for outer Saginaw Bay cannot be well correlated with the fraction of diatoms present means that the constant ratio assumption for this part of the bay is reasonable unless another variable can be shown to influence the ratio.

The division of phytoplankton into diatom and non-diatom fractions, although simplistic, was successful in explaining a major part of the variability in the data. Further divisions could probably be made to improve the correlation. The cruise in early July (Cruise 10) had the highest chlorophyll *a* to biomass ratio, and it is during this time when green algae were found to be a sizeable fraction of the total crop (Figure 4b). In Lake Kinneret, the ratio of chlorophyll to fresh weight biomass was found to change significantly during blooms of the dinoflagellate *Peridinium* (Berman and Pollingher 1974).

Although the correlation with fraction of diatoms explains a good deal of the variance of the chlorophyll *a* to biomass ratio, further factors must be included to confidently predict the ratio. This is obvious when different cruises with very similar fraction diatoms are compared (Table 8). Such factors would probably include cell nutrient concentrations, light intensity during growth period, age of cells and water temperature. However, in enriched waters, species composition appears to be the dominant factor.

Enriched areas are often the major target of modeling studies because of concerns about water quality degradation. The question of which quantity best represents phytoplankton abundance must be answered before intelligent decisions on which type of model to use can be made. In addition, some complex water quality issues, such as taste and odor problems and species shifts, must be addressed by species or group specific models regardless of the state of enrichment of the water body in question. If development of multi-class phytoplankton production models is to continue, a standardized method of measuring cell counts and volumes will be necessary. There are, at present, considerable problems caused by differences in counting units and methods (Tarapchak and Stoermer 1976). If methods can be standardized, then the choice of an indicator of algal abundance will be less difficult.

TABLE 8. Observed vs. calculated natural logarithm of the ratio of chlorophyll a to biomass for cruises with similar fraction diatoms.

	Fraction Diatoms By Volume	Calculated Ratio	Observed Ratio
Segment 1			
Cruise 8	.9338	1.40	1.26
Cruise 16	.9389	1.39	2.03
Cruise 10	.1892	2.92	3.22
Cruise 11	.1838	2.93	2.69
Segment 2			
Cruise 10	.2015	2.98	3.69
Cruise 12	.2033	2.97	2.53

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